

FIELD TRIP GUIDE TO THE LA RIOJA FOSSIL TRACKSITES

INTERNATIONAL SYMPOSIUM ON DINOSAURS AND OTHER VERTEBRATES PALEOICHOLOGY

Fumanya-Esperáza (Spain, France)

October 3-9, 2005

By

Joaquín Moratalla and Javier Hernán



Instituto Geológico y Minero de España (Museo Geominero). Ríos Rosas, 23, 28003 Madrid (Spain).



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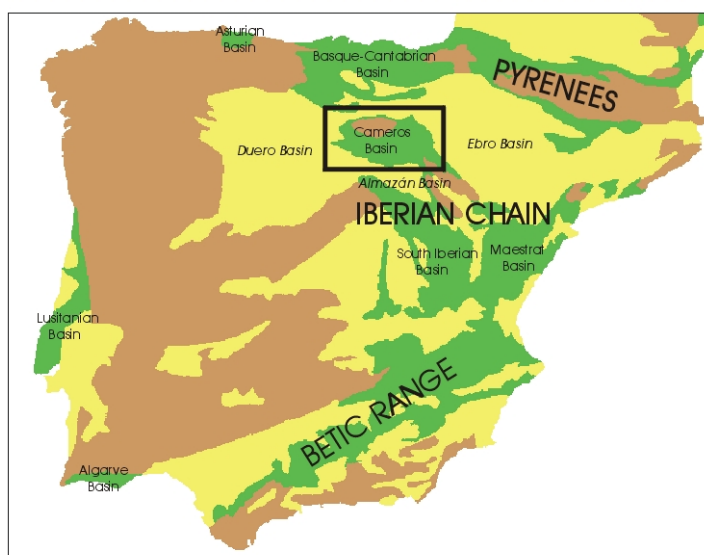
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The relative scarcity of vertebrate bone remains from the Cameros Basin oblige us to study the bio-diversity mainly based on the track fossil record. This fact represents an indirect method for evaluating the faunal composition of the past. So, the study of fossil tracks is useful not only in order to obtain information about locomotion, behavior, etc. but, as in the case of several basins like Cameros, to carry out an indirect analysis on diversity, ecosystem balance, animal relationships, paleoenvironment aspects, etc. Otherwise, we would not have information about the general composition of the Lower Cretaceous faunas from the Cameros Basin.

THE CAMEROS BASIN

The Cameros Unit (or Massif), located in the north-westernmost part of the current Iberian Chain, was developed by the tectonic inversion of the late Jurassic-early Cretaceous Cameros basin. Nowadays, this unit constitutes a mountain range roughly situated between two important Paleozoic Massifs: the Sierra de la Demanda in the northwestern (San Lorenzo, 2 262 m) and the Sierra del Moncayo in the southeastern (Moncayo, 2 315 m). This zone is included within the provinces of Soria and Burgos (Autonomic Community of Castilla-León) and La Rioja (Autonomic Community of La Rioja).



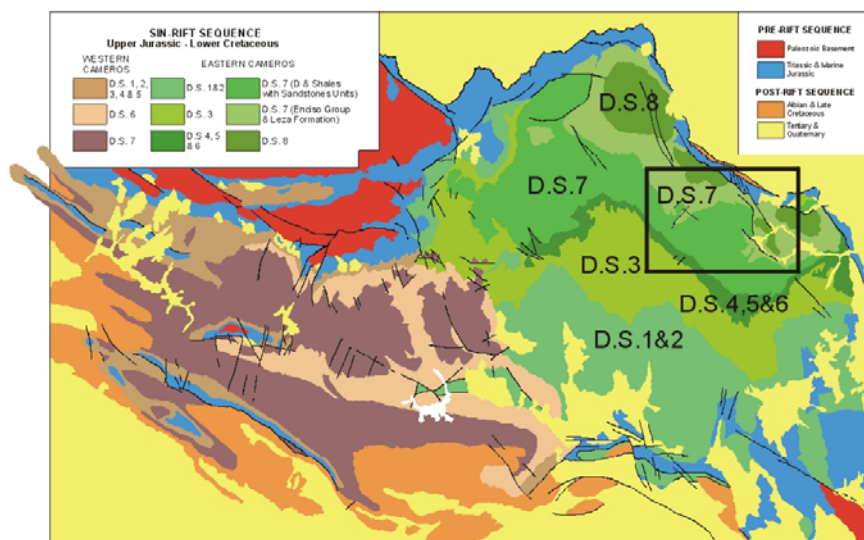
Location of the Cameros basin

This unit belongs to the present Iberian Chain: an alpine intraplate fold-and-thrust belt of moderate intensity located in the eastern Iberian Peninsula. It lies in an intermediate position between two main alpine orogenic belts which were developed in the paleomargins of the Iberian Plate: the Betic Chain to the south and the Cantabrian Range-Pyrenees to the north.

The northern border is bounded by the North Cameros thrust: a roughly east-west-trending thrust which overthrusts the Cameros Unit over the Oligocene-Miocene

deposits of the present foreland Ebro basin. South-eastwards, it is covered by the Ebro basin deposits, but its subsurface trace can be deduced until the Iberian and Catalanian Coastal Chain, therefore, being the prolongation of the North Iberian thrust (Guimerà et al., 1995; Salas et al., 2001; Guimerà et al., 2004). The inferred horizontal displacement is about 15-30 km (Casas Sainz, 1993; Guimerà et al., 1995; Muñoz Jiménez and Casas Sainz, 1997). The southern boundary is settled by the South Cameros thrust that is formed by a system of imbricated thrust, folds and faults overthrusting the Cameros Unit over the Tertiary Duero and Almazán basins (Morillo and Meléndez Hevia, 1972; Platt, 1990; Miegobille et al., 1993). Therefore, because of a longer displacement of its northern border with regard to the southern one, the Cameros Unit displays an asymmetric pop-up structure about 80 km wide (Guimerà et al., 1995; Guimerà, 2004).

During the second rifting cycle of the Mesozoic Iberian Rift System, four strongly subsident basins were generated: 1) Columbrets basin in the offshore Mediterranean; 2) South Iberian basin; 3) Maestrat basin (Oliete, Penyagolosa, La Salzedella, Morella, El Perelló, Aliaga, Galve, Las Parras and Aguilón sub-basins) and; 4) Cameros basin (Eastern and Western Cameros sub-basins). Their structural and sedimentological evolution were strongly influenced by the North Atlantic spreading and the progressive opening of the Bay of Biscay (Salas et al., 2001).



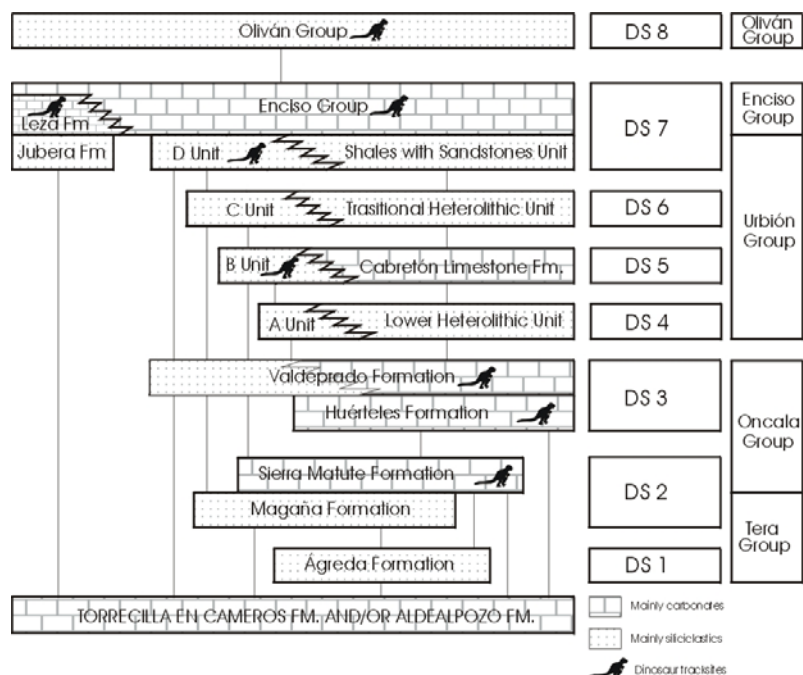
Map of the Cameros basin

The Cameros basin is an atypical basin within the context of the Mesozoic Iberian Rift System because its anomalous high subsidence and sedimentation rates and, also because is the only one in which part of the infill has been affected by metamorphism (Guiraud and Seguret, 1985; Golberg et al., 1988; Casquet et al., 1992; Mas et al., 1993; Barrenechea et al., 1995; Alonso Azcárate et al., 1995).

The Cameros basin can be divided into two sub-basins with different tectonic and stratigraphic framework: 1) the Eastern Cameros sub-basin, about 80 km long and 60 km wide, has an extremely thick sedimentary pile of sediments (up to 9000 m) and; 2) the Western Cameros sub-basin, up 115 km long and 50 km wide, with a maximum thickness in depocentral areas of about 3000 m (Mas et al., 1993; Martín Closas & Alonso, 1998).

Stratigraphic framework

As seen before, the Cameros basin can be divided into two sub-basins, each with a rather different stratigraphic framework. Several lithostratigraphic schemes have been proposed for the Eastern Cameros infill. Tischer (1966a, b) performed the first important stratigraphic study of this sub-basin which still keep certain grade of validity and defined five lithological Groups: Tera, Oncala, Urbión, Enciso and Oliván. Subsequently, others authors have modified it (Salomon, 1982a, b; Guiraud, 1983;



General Stratigraphy of the Eastern Cameros sub-basin

Guiraud and Seguret, 1985), nevertheless, nowadays the stratigraphic scheme is based in depositional sequences (Mas et al., 1993; Martín Closas and Alonso, 1998; Alonso Azcárate et al., 2005).

Therefore, the latest Jurassic-early Cretaceous depositional megasequence of the Cameros basin is mainly constituted by deposits of continental origin with sporadic marine incursions. This megasequence is bounded by two main discontinuities of regional extend: the lower is early Tithonian and the upper is early Albian in age. The synrift sedimentary infill comprises eight depositional sequences in the Eastern and seven in the Western Cameros sub-basin, each one is further separated by minor discontinuities (Alonso et al., 1991; Mas et al., 1993; Martín Closas and Alonso, 1998; Alonso Azcárate et al., 2005). In this paper, it is only going to be briefly commented the units of the Eastern Cameros sub-basin.

The **Depositional Sequence 1** (Tithonian), representing the onset of the initial rift phase, constitutes the north-westward spread of the Iberian rifting as far as the Cameros basin and comprises the Ágredda Formation.

The **Ágredda Formation** involved the beginning of the faulting that gave rise to an important tectonic and sedimentary modification. This formation crops out in two non-connected sedimentary areas with important and different subsidence rates. The first one, denominated "Torrecilla basin" (up to 73 m thick), consists of clastic-dominated deposits with some carbonate beds, corresponding to a meandering fluvial system with carbonate pools. The second one, "Ágredda trough" (up to 255 m thick), comprises mainly siliciclastics and scarce limestones interpreted as alluvial fans linked to basin-bounding faults with source area in the "Moncayo Massif", passing southwards into alluvial plains with meandering rivers and small carbonate lakes (Gómez Fernández, 1992; Gómez Fernández and Meléndez, 1994a).

In the **Depositional Sequence 2** (upper Tithonian?-lower? Berriasian) two units are distinguished, a lower of fluvial origin called the Magaña Formation and an upper unit, fluvial-lacustrine, the Sierra de Matute Formation.

The **Magaña Formation** (up to 695 m thick) is a detritic-dominated succession interbedded with minor and localized limestone beds. This unit displays a new tectonic and structural setting of the basin, just as a change of the source area located into the “Castilian Massif”. It represents a west-to-south flowing fluvial system, with gravel to sandstone braided rivers passing to fine-grained meandering and floodplain deposits (Gómez Fernández, 1992; Gómez Fernández and Meléndez, 1994a). The **Sierra de Matute Formation** (up to 646 m thick) is a heterogeneous mixture of detritic-carbonate deposits, predominating slightly the carbonates. This unit involved a new tectonic distribution of the basin and was related to a sea level rise as is proved by some marine contaminations. It is interpreted as a braided to meandering system with lacustrine and palustrine environments to the south-eastern with its source area in the Demanda Massif (Normati and Salomon, 1989; Schudack and Schudack, 1989; Gómez Fernández, 1992; Gómez Fernández and Meléndez, 1994a).

The **Depositional Sequence 3** (Berriasian) is represented by a basal essentially lacustrine unit, denominated Huérteles Formation, which grade upward into the fluvio-lacustrine Valdeprado Formation.

The **Huérteles Formation** (up to 1050 m thick), deposited in a strongly subsiding NW-trending trough, displays a mixed siliciclastic-carbonate record increasing its carbonate content upward and eastward. This formation is interpreted as a playa-lake system with bajada environment passing to the east into sandflat and mudflats with ephemeral lakes. In the easternmost part, there was a perennial saline lake with fan-deltas from the north-eastern basin-bounding faults ("Ebro Massif") (Gómez Fernández, 1992; Gómez Fernández and Meléndez, 1994a, b). The **Valdeprado Formation** (up to 1164 m thick), exhibiting a tectonic-related sedimentation, was deposited in two NW-trending troughs, and comprises another continental carbonate-terrigenous mixed unit with scarce marine intrusions. This formation was deposited in a west-to-east flowing fluvial system with braided and meandering rivers discharging into a carbonate lake in the easternmost part. The source area is located in the denominated "Castilian Massif" (Gómez Fernández, 1992; Gómez Fernández and Meléndez, 1994a).

The **Depositional Sequence 4** (latest Berriasian-Valanginian) consists of two laterally related fluviatile units: the A Unit and the Lower Heterolitic Unit.

The **A Unit** (up to 200 m thick) is a siliciclastic-dominated succession corresponding to a fluvial meandering and floodplain system (Barrenechea, 1994; Barrenechea et al., 1995). The **Lower Heterolitic Unit** (up to 40 m thick), conforming a complete fluviolacustrine cycle, is a siliciclastic-carbonate unit deposited in the south-eastern low part of the sub-basin. It is interpreted as a fluviatile system with wide lacustrine and palustrine areas (Salinas and Mas, 1990).

The **Depositional Sequence 5** (late Hauterivian-early Barremian) consists of two laterally interfingered lithostratigraphic units: the B Unit and the Cabretón Limestone Formation.

The **B Unit** (up to 500 m thick) outcrops only in the central area and is typically composed of fine-grained siliciclastic deposits and locally intercalated scarce carbonate strata. It was deposited in a wide meandering floodplain system developing significant shallow carbonate lacustrine complexes easternward (Barrenechea, 1994; Barrenechea et al., 1995). The **Cabretón Limestone Formation** (up to 35 m thick) consists mainly of carbonate deposits representing a well developed carbonate lacustrine system (Tischer, 1966a, b; Salinas and Mas, 1990).

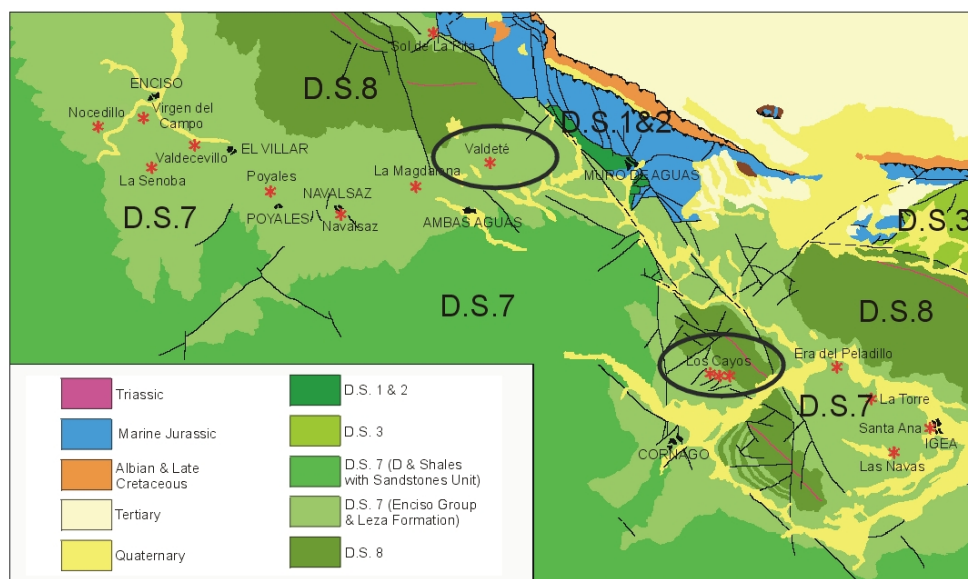
The **Depositional Sequence 6** (Barremian) involves an important tectonic reactivation of the basin and is composed of two lateral-related units: the C Unit and the Transitional Heterolitic Unit.

The **C Unit** (up to 900 m) is made up of fine-grained siliciclastic sediments deposited in a meandering fluvial system (Barrenechea, 1994; Barrenechea et al., 1995). The **Transitional Heterolitic Unit** (up to 100 m) is a carbonate-terrigenous succession decreasing its carbonate content upward. It was

deposited in a lacustrine complex passing upward into fluvial one (Salinas and Mas, 1990).

The **Depositional Sequence 7** (late Barremian-early Aptian) exhibits a basinwide distribution and is composed of five lateral and vertically-related units: D Unit, Shales with Sandstones Unit, Jubera Formation, Leza Formation and Enciso Group.

The **D Unit** (up to 150 m thick) is composed of siliciclastic-dominated sediments which correspond to a NW-to-SE-flowing fluvial system passing from braided to meandering and floodplain deposits (Barrenechea, 1994; Barrenechea et al., 1995). The **Shales with Sandstones Unit** (up to 100 m thick) comprises fine-grained terrigenous deposits which are interpreted as a meandering fluvial complex (Salinas and Mas, 1990). The **Jubera Formation** (up to 215 m) only occurs in the north-eastern margin of the basin. It consists of siliciclastic sediments interpreted as alluvial fans at fault-bounded northern edge of the basin with Paleozoic and Jurassic rocks as source areas (Alonso and Mas, 1993). The **Leza Formation** (up to 400 m thick) is composed of carbonate-dominated deposits outcropping along the north-east border into six lithosomes bounded by faults. It is interpreted as carbonate coastal lacustrine systems with intermittent



Location of the Valdeté and Los Cayos tracksites

marine intrusions from the Tethys (Alonso and Mas, 1993). The **Enciso Group** (up to 1500 m) comprises a siliciclastic-carbonate cyclic alternation corresponding to a large perennial lacustrine lake (Doublet et al., 2003; Doublet and Garcia, 2004).

The **Depositional Sequence 8** (late Aptian-early Albian) involved a new tectonic reactivation of the basin and comprise one unit called the Oliván Group.

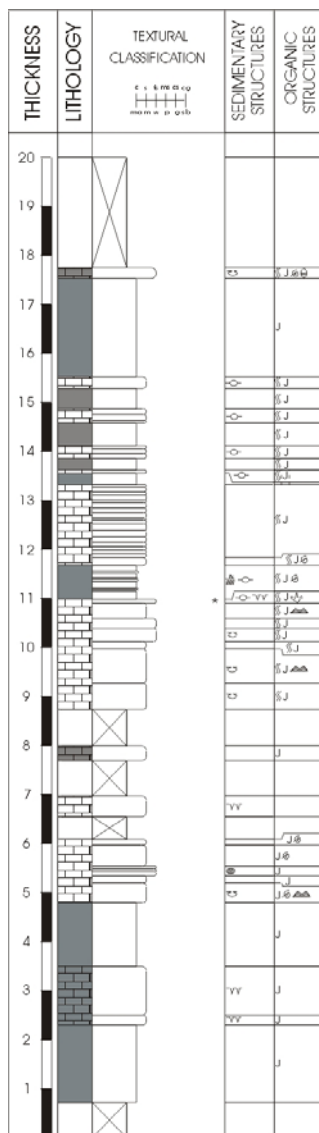
The **Oliván Group** (up to 2000 m thick) consists of siliciclastic materials that were deposited in a meandering and related floodplain fluvial system (Tischer, 1966a, b; Guiraud and Seguret, 1985).

We will visit in this field trip three dinosaur tracksites of the Rioja province. Whereas Valdeté (Préjano) and Los Cayos (Cornago) are included in the Enciso Group (Depositional Sequence 7), Virgen del Prado (Inestrillas-Aguilar del Río Alhama) is included in the Oncala Group (Sierra de Matute Formation) (Depositional Sequence 2). So, this last tracksite is, up to now, one of the most ancient localities of the Cameros basin.

THREE DINOSAUR TRACKSITES

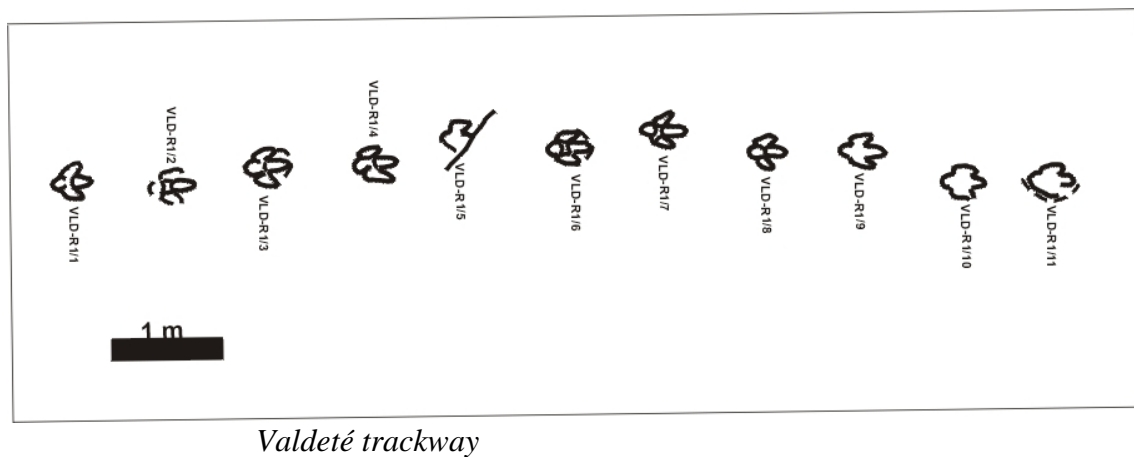
Valdeté Tracksite

The Valdeté tracksite is located in the township of Préjano (La Rioja province). The stratigraphy is dominated by a series of calcareous layers interpreted as deposited in a lacustrine environment. The tracksite has yielded a unique trackway formed by 12 footprints, although the last one (number 12) is very bad preserved and even not included in the figure. The trackway (VLD-R1) is relatively well preserved. However, the footprint VLD1-R1/5 is almost completely eroded: due to the presence of a crack on the layer surface and only the posterior heel and digit IV outline can be observed.



Stratigraphic section of the Valdeté tracksite

The footprints are tridactyl with a well defined outline. Their length (mean value: 41.3 cm) is higher than the width (mean value: 33.2). So, the Length/Width ratio is relatively high: 1.24. The digits are wide, strong and relatively elongated with their distal ends relatively rounded. The digit III is more developed than the other ones (mesaxonic condition) and it is U-shaped. The lateral digit (IV) is more developed (9.5%) than the medial digit (II). The hypexes show a symmetrical disposition, that is, the distance between both hypexes and the distal heel end is more or less the same. Each digit and the heel surface contain one pad impression. The heel outline is well rounded and it shows a well defined outline. Both interdigital angles are relatively low (II-III: 25.7°; III-IV: 23.6° as mean values). Some footprints (VLD-R1/3, VLD-R1/6 and



VLD-R1/11) have a front depressed area, except for the distal heel zone.

The trackway has a direction of movement of 90° E showing a relatively straight pattern. The stride length is relatively constant throughout the trackway. However, the pace values for the right-left feet are about a 13% shorter than those belonging to the left-right feet. In front of the track VLD-R1/6 we can observe a short and curved groove. It begins about 8 cm in front of the digit IV.



Valdeté tracksite: Footprint VLD-R1/3



Valdeté tracksite: Footprint VLD-R1/7

The Valdeté footprint morphology is interesting. On one hand, the digits (wide and with rounded distal ends) suggest the presence of an ornithopod trackmaker. The



same conclusion could be inferred from the heel outline, the symmetrical heel indentations or the presence of one pad impression for each digit. On the other hand, the high value of Length/Width ratio indicates a footprint relatively elongated, more typical of the variability produced by theropod dinosaurs.

Moratalla (1993) tentatively proposed that a camptosaurid dinosaur, probably a form similar to the European species *Camptosaurus prestwichii*, could have produced this trackway. However, this hypothesis is, right now, very debatable. In fact, the fragmentary condition of *C. prestwichii* obliges us to reconsider and to make a more deep analysis among the European Lower Cretaceous ornithopods.

The presence of a slight depression in front of some of the Valdeté footprints could suggest some kind of interdigital web for the autopodia. However, this idea seems not to be possible due to this area is present beyond the distal digit ends. The little groove located just in front of VLD-R1/6 print could be explained by two alternative hypothesis: 1) a caudal mark; 2) a manus impression. While the curve morphology of that impression would be accord with a caudal mark, in contrast, its location would be according with a manus dragging event. Although both hypothesis would probably be possible, the location is similar to those of some quadrupedal ornithopod trackways from the Cameros Basin (Moratalla et al., 1992a; Moratalla et al., 1994).

One of the most striking characters of this trackway is related to the different values of the right and left pace distances. This locomotion pattern (limping) is typical of those animals that present some kind of foot or limb injury. The injury would be responsible of the limping behavior. However, no anatomical differences can be observed among right and left footprints.

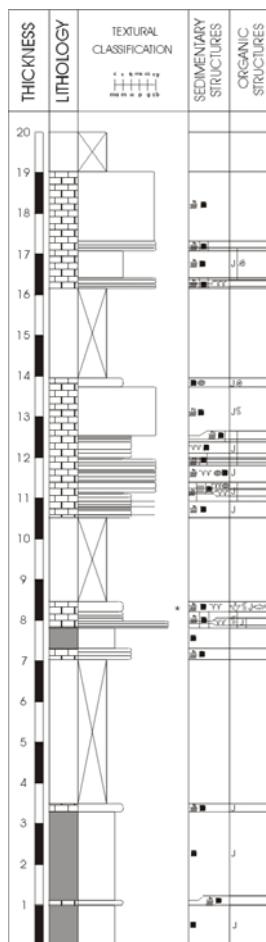
Virgen del Prado tracksite

The Virgen del Prado outcrop is located very near of the homonymous church (township of Inestrillas-Aguilar del Río Alhama, La Rioja province). The track bearing layer is a calcareous dark massive stratum of about 40 cm in thickness belonging to the Sierra de Matute Formation (Oncala Group). Some scattered holostean scales, turtle plate fragments and crocodile teeth can be observed on the top of the layer.



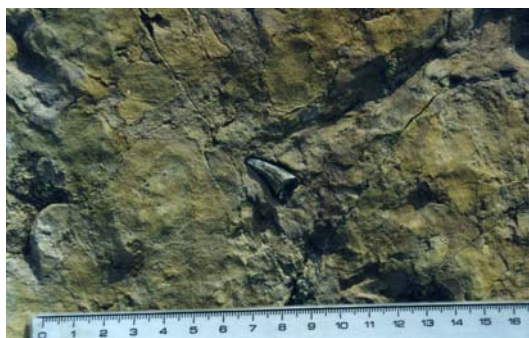
Virgen del Prado (Inestrillas-Aguilar del Río Alhama)

The track bearing layer shows an inclination of 34° , and an extension of about 50 x 6 m. It has yielded about 200 footprints, mostly isolated tracks and 6 trackways. The size of the Virgen del Prado tracks ranges from 30 to 32 cm in length. The digits are very long and narrow and sometimes slightly curved. No heel indentations or pad impressions can be observed. Interdigital angles are very high. The heel surface is highly transversely and longitudinally reduced. The heel outline is sometimes posteriorly elongated. The mean stride length is of about 2 m.

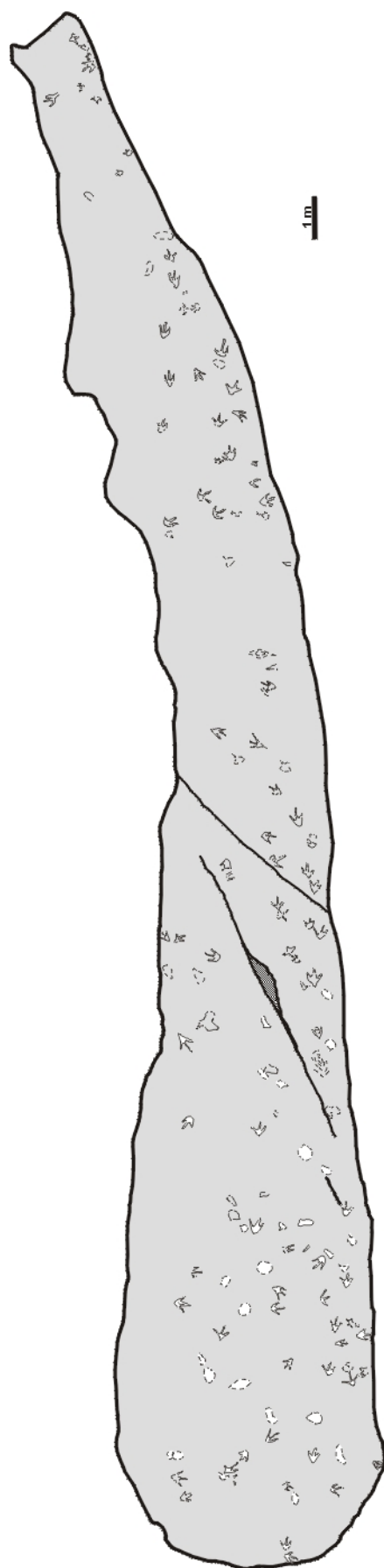


Stratigraphic section of the Virgen del Prado tracksite

The extremely narrow condition of some digits could be caused by preservational hazards. However, relatively similar tracks have been reported from other localities of the Oncala Group, suggesting that theropods with relatively gracile feet and slender toes were relatively abundant throughout the Cameros Basin during the Oncala times.



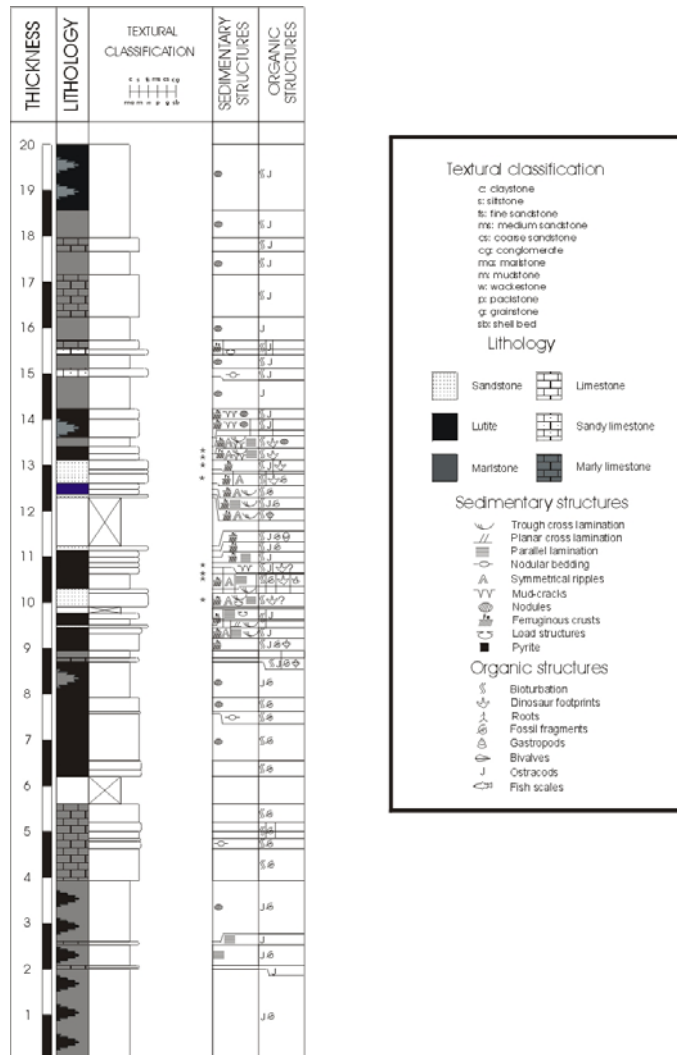
Crocodile tooth on the surface of Virgen del Prado outcrop



Virgen del Prado
Inestrellas-Agnilar del Río Alhama
(La Fioja)

Los Cayos area

The Los Cayos area (township of Cornago) is constituted, up to now, by at least 6 tracksites making one of the most spectacular and well preserved zones of the European fossil record. This area is located approximately 1.5 km north of Cornago town and it has a very easy access for the visitors. The sediments (sandstone, limolites, carbonates and silstones) are included in the Enciso Group (Lower Aptian in age), about 115 ma BP.



Los Cayos stratigraphic section

Although theropod dinosaurs produced most part of the Los Cayos footprints, there are also other tracks evidencing a relatively high bio-diversity. So, Los Cayos has also yielded tracks of ornithopods (Los Cayos D), sauropods (Los Cayos A and S), turtles (Los Cayos C), and pterosaurs (Los Cayos A and C).



Los Cayos A (Cornago)

Theropod tracks

The theropod tracks are the most abundant of the Los Cayos tracksite (about 95%). These tracks are present in most of the outcrops: Los Cayos A, B, C, E and S.

The Los Cayos A site is formed by a stratigraphical surface of about 1200 m². The dinosaur tracks are exceptionally well preserved. Sometimes their depths are more than 10 cm. Although some tracks still have part of the infill sediment, most of the



Isolated theropod footprint from Los Cayos A (Cornago)

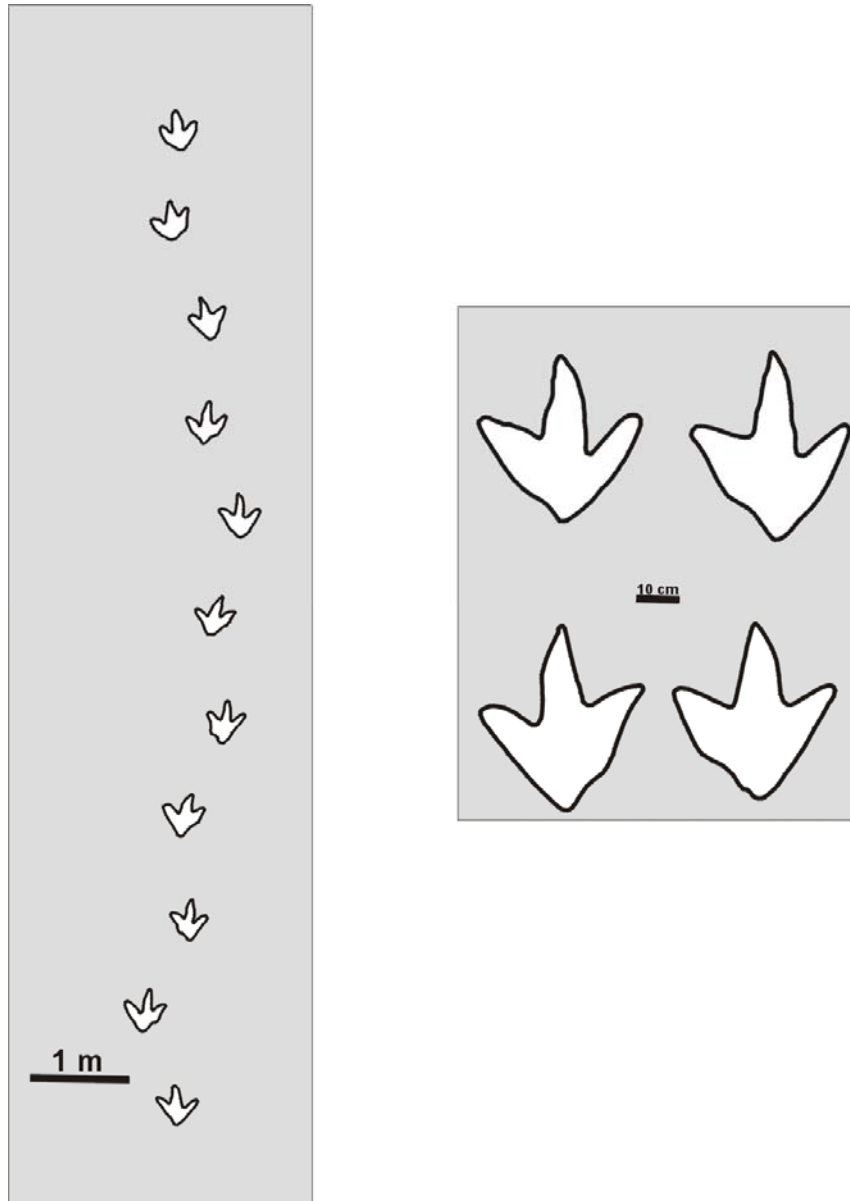
Los Cayos footprints constitute conspicuous examples of dinosaur track molds. Although there is some morphological variability, most of the Los Cayos dinosaur footprints show the same general features, suggesting that they were produced by a similar kind of animal. 36 dinosaur trackways can be observed at Los Cayos A outcrop (193 tracks). Moreover there are 232 isolated tracks. The total number of footprints is 425.



Partial view of the Los Cayos A site (Cornago)

The longest trackway (LCA-R3) is formed by well preserved 11 footprints. The number 4 is exceptionally well preserved. Its length is 44 cm and its width, 42 cm. So, the length/width ratio is 1.07. The digits are relatively broad, strong, and distally acuminate. The central digit (III) is clearly V-shaped and slightly medially curved. The digit II is also medially curved while the digit IV is straight with a lateral orientation. The II-III angle is 32° and the III-IV angle is 35°. The heel surface is relatively broad showing a medial indentation. The deeper areas inside the footprint are located in the digit III and in the heel, suggesting a mesaxonic impression.

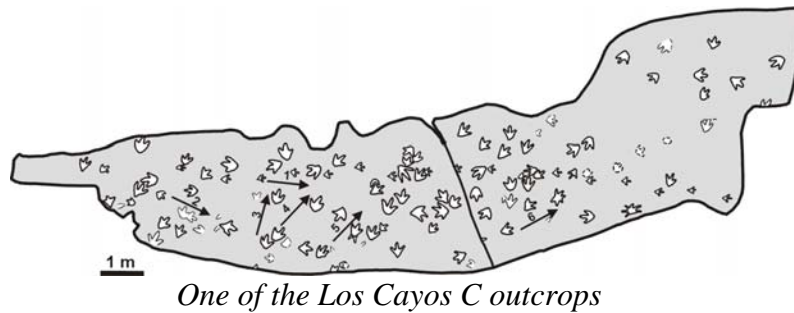
Most of the theropod tracks of the Los Cayos area are tridactyl. However, some of them show hallux impression. These hallux tracks show a more longitudinal heel outline, suggesting that the position of the metacarpus during the locomotion were more horizontal than those causing the tridactyl ones.



Trackway LCA-R3 (Los Cayos A tracksite)

This general morphology of the Los Cayos A dinosaur footprints could be extended also to the Los Cayos B and C ones. The Los Cayos B (level 1) is a 450 m² of relatively coarse sandstone with about 250 theropod tracks, 69 of them constituting 10 trackways. However, the level 2 is formed by a fine limolite that has registered nice dinosaur tracks. One of the trackways (with 17 footprints) is formed by relatively small tridactyl prints (16-18 cm in length). The morphology is relatively different than that of the other theropod tracks: the distal end of the digits is more rounded, the digit III outline show parallel borders, and a more symmetrical and reduced heel surface. Although we consider this trackway as caused by a theropod dinosaur, it is difficult to

conclude if it is a juvenile dinosaur or an adult small form. Future research should be done about this issue.



Moratalla (1993) identified the Los Cayos theropod footprints as the ichnogenus *Buckerburgichnus* Abel 1935. However, Lockley et al., (1996, 1998) questioned this interpretation suggesting the use of the name *Megalosauripus*. Only one trackway at Los Cayos C could be identified as the ichnogenus *Therangospodus* (Moratalla, 1993; Lockley et al., 1998). Regardless of the use of *Buckeburgichnus* or *Megalosauripus* name, the evidence suggests that the theropod tracks of the Los Cayos area belong to at least three theropod footprint morphotypes.

Ornithopod tracks

Los Cayos D is only the outcrop that has yielded ornithopod tracks. It is a bioturbated surface of about 130 m² of a sandstone. This outcrop had about 90 tridactyl footprints some of them still containing the infill sediment. Most of the tracks are



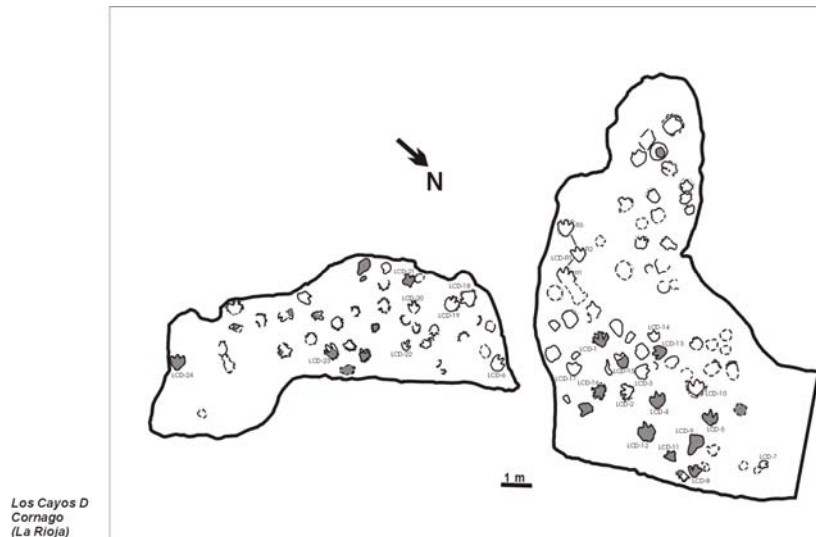
Los Cayos D (Cornago)



Isolated footprint

isolated and only one trackway with 3 footprints can be observed. This trackway shows short paces and stride, low angle pace and a high inward rotation values. Some of the tracks are very deep showing high and well-defined displacement rims. The best-

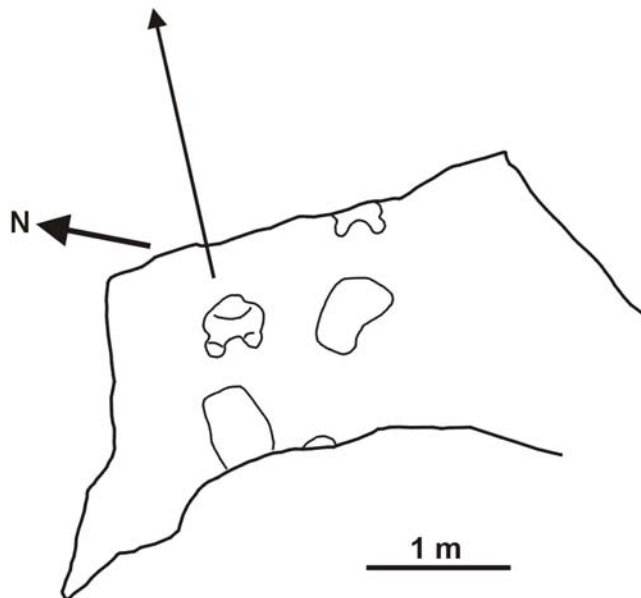
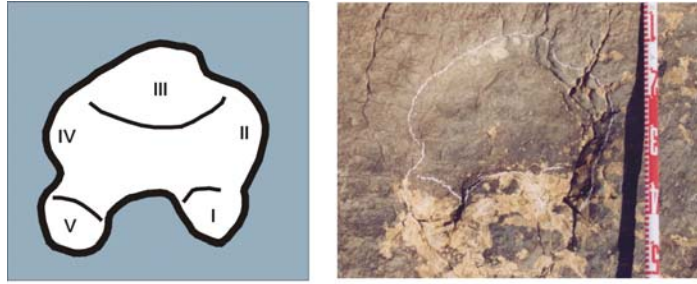
preserved footprints show a length that ranges between 60 and 65 cm. The digits are very wide, short and with rounded distal ends. The heel surface is very broad, and the heel outline broad and rounded. Two slight indentations can be observed in both sides (medial and lateral).



These Los Cayos D footprint features suggest that ornithopod dinosaurs belonging to the Iguanodontidae clade made the tracks.

Sauropod tracks

Despite of some sauropod manus impressions (probably underprints) found at Los Cayos A site, the Los Cayos S tracksite is the only outcrop of the Los Cayos area that has yielded sauropod prints. The main level shows a sauropod trackway fragment formed by five prints. Footprints are about 50 cm in length and about 37 cm wide. These footprints are very shallow, and they have no digit impressions. On the contrary, the manus prints are more deep impressed on the sediment. Only one manus print is completely preserved. It is half moon shaped, showing a length of 32 cm and a width of

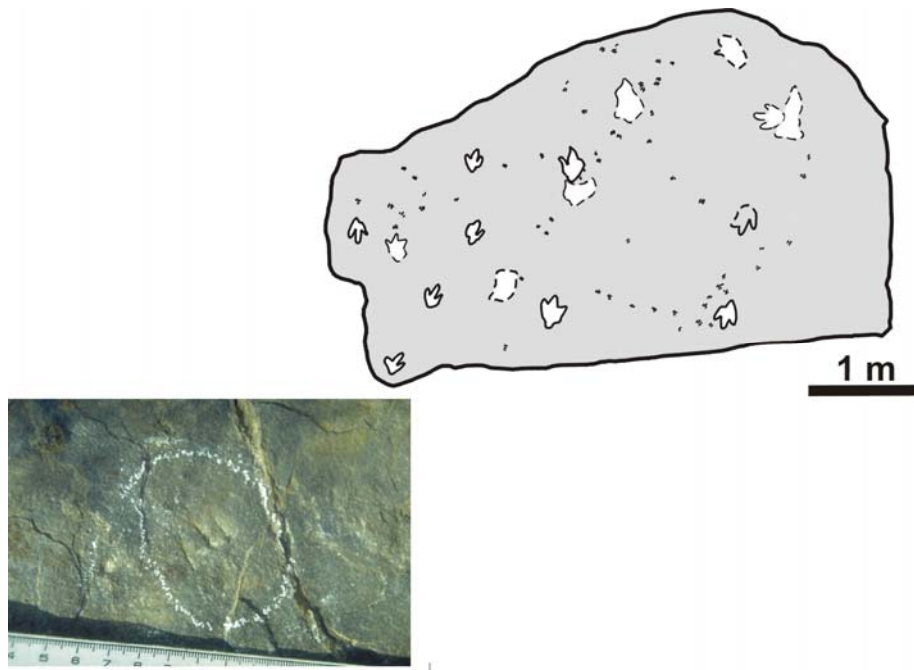


Sauropod manus print from Los Cayos S (Cornago)

37 cm. The digits I and V are clearly rounded. The digits II and IV are clearly visible and the digit III area is relatively broad, about 25 cm wide. The angle between the digits I and V is very high, more than 270° . These features suggest that the trackmaker would be a Titanosaurid or Titanosauriform sauropod.

Turtle tracks

One of the Los Cayos C exposures has yielded 16 relatively well preserved theropod footprints and 58 tiny impressions that have been identified as turtle tracks. No trackways can be observed although some alignments could be pointed out. The print length ranges from 0.5 to 1.5 cm. The digit marks are isolated, showing a parallel disposition, and with distal ends clearly acuminate. Turtle tracks are not very abundant in the fossil record (Bernier et al., 1982, 1984; Moratalla et al., 1992b; Foster et al., 1999;

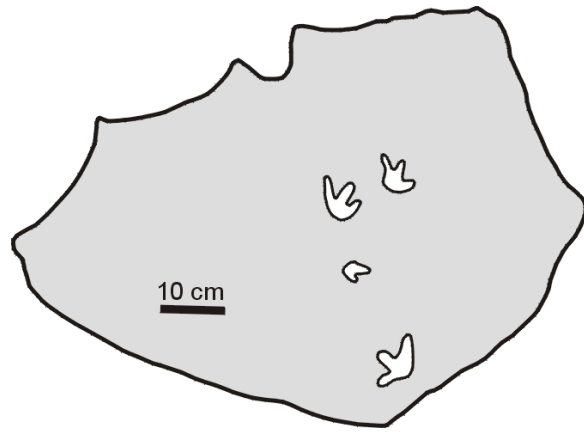
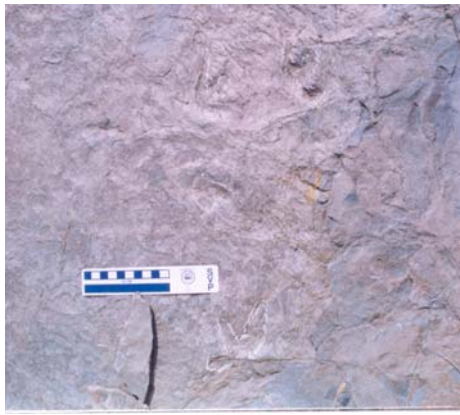


Turtle tracks from Los Cayos C (Cornago)

Wright & Lockley, 2001) and the shape and size of these Los Cayos turtle prints do not allow us to identify the trackmaker. Moreover, these features suggest that the prints were caused by buoying activities more than a clear terrestrial locomotion pattern. This interpretation would explain the parallel digit impressions and the absence of complete tracks. In any case, the presence of turtle tracks in Los Cayos seems to be paleoecologically significant, with turtle and dinosaur prints on the same sedimentary level.

Pterosaur tracks

Los Cayos A and C have yielded some isolated pterosaur manus prints. A little slab at the Los Cayos A shows 4 manus tracks and the Los Cayos C only one specimen. They are small in size, tridactyl, asymmetrical and with the digit III more developed than the other ones. The interdigital angles ranges from 120° to 130°. No footprints or trackways have been found yet. The Cameros Basin seems to be a good area for pterosaur tracksites. More than 20 localities have been described (Lockley et al., 1995; Fuentes & Meijide, 1996; Pacual & Sanz, 2000). All the specimens, even those we describe herein, have been identified as the ichnogenus *Pteraichnus*. Most of the tracks are manus prints, but some footprints and trackways have also been described. The pterosaur tracks in the Cameros Basin are more abundant in the Oncala Group (Tithonian-Berriasian in age). In fact, the Los Cayos pterosaur tracks are the only ones



Pterosaur tracks from Los Cayos A (Cornago)

that have been reported from the Enciso Group (Lower Aptian). The presence of pterosaur tracks in the Cameros Basin suggests two interesting consequences: 1) the

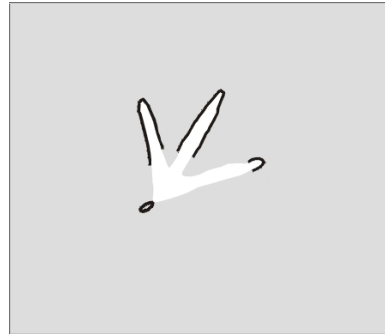


Pterosaur manus print from Los Cayos A (Cornago)

pterosaurs were important dwellers of the Cretaceous continental ecosystems of the Cameros region, and 2) their terrestrial abilities were more developed than we previously had been considered.

Avian-like footprints

Some scattered and not well preserved avian-like footprints have been described at the Los Cayos C site. The best preserved specimen has 2 cm in length and it shows isolated digit impressions. The digits are long and narrow, with acuminate distal ends.



Avian-like footprint from the Los Cayos C (Cornago)

The proximal digit areas, the hypexes, and the heel surface are not preserved. A significant feature of this track is the presence of a posterior digit mark caused by the hallux (digit I). This impression shows a postero-medial orientation with an angle I-III of 160° . The retroversion of the hallux has been considered an avian feature although more recently Middleton (2002) has suggested that the posterior orientation of the digit I is not present in primitive birds. However, the evidence of this Los Cayos C track suggests, at least, an avian-like footprint morphology. If this hypothesis were correct, Los Cayos C would be a special tracksite, with non avian dinosaurs, avian dinosaurs, turtles and pterosaurs in the same sedimentary levels.

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